

# PERCENTAGE SEED SET, SPROUTING HABIT AND PLOIDY LEVEL IN *ARCTOSTAPHYLOS* (ERICACEAE)

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## ABSTRACT

Comparisons of sprouting and nonsprouting, diploid ( $2n$ ) and tetraploid ( $4n$ ) *Arctostaphylos* species revealed that reduced seed set was associated with tetraploidy in addition to the sprouting habit. When sprouting and nonsprouting species were combined, percentage seed set values, measured as seed to ovule ratios, were significantly higher for  $2n$  species than for  $4n$  species ( $P < 0.01$ ), but when  $2n$  and  $4n$  species were combined, comparisons between sprouting and nonsprouting species were not significantly different. Sprouting  $4n$  species consistently had the lowest seed set values. These results have important implications for interpretation of comparative life history studies among sprouting and nonsprouting *Arctostaphylos* species.

Comparative seed bank studies of post-fire sprouting and non-sprouting *Arctostaphylos* species have reported lower seed viability, and consequently lower viable seed bank densities among sprouters (Keeley 1977, 1987; Kelly 1986; Kelly and Parker 1990). All sprouters examined in the above studies, however, were tetraploid whereas the nonsprouters were diploid (Wells 1968). (Most *Arctostaphylos* sprouters are tetraploid.) Thus, lower number of viable seeds seems to be associated with two characteristics, ploidy level and life history (sprouting and nonsprouting).

Differences among sprouters and nonsprouters in several papers have favored nonsprouters, and have often been interpreted as being the result of differential life history selection (Carpenter and Recher 1979; Fulton and Carpenter 1979; Parker 1984). However, the conclusions reached in the studies favoring nonsprouters have not always been consistent with regard to differences between sprouters and nonsprouters in seed production or persistent seed bank sizes in other studies (e.g., Keeley 1977; Lamont 1985; Kelly and Parker 1990; Cowling et al. 1987). These inconsistencies may result from factors not taken into account, such as reduced seed set. We propose that for *Arctostaphylos* species, lower seed numbers among sprouters is associated with ploidy rather than the sprouting character. The purpose of this study, therefore, was to test the null hypothesis that tetraploid and diploid *Arctostaphylos* species set the same percentage of seeds regardless of their ability to sprout.

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## METHODS

Seed to ovule ratios were used to estimate seed set for fourteen (1986) and seven (1987) sprouting and nonsprouting *Arctostaphylos* species from widely separated locations in California. Ratios were determined by dividing the mean number of seeds per fruit by the mean number of ovules per ovary. The ovaries and fruit used were only those not damaged by insects or any other outside forces. Seeds were counted only if they were plump and white, which indicates a viable seed. Sample sizes were determined by availability and varied from 10 to 100 for ovaries, and 10 to 50 for fruit. Flowers and fruit were collected at the peak of flowering or fruiting season, from all sides of the plants, and from at least 10 different plants at each location or as many plants as were bearing flowers or fruit.

To avoid differences due to environmental limitations, we examined species from widely separated locations, and as much as possible, we chose sites that contained more than one species, preferably, species that differed in ploidy. The species examined, their ploidy level (Wells 1968) ( $2n$  = diploid,  $4n$  = tetraploid), mode of reproduction (S = sprouting, NS = nonsprouting), locations and respective elevations were: *A. patula* E. Greene ( $2n$ , S) and *A. mewukka* Merriam ( $4n$ , S) from Peavine Ridge, El Dorado County (1600 m); *A. stanfordiana* Parry ( $2n$ , NS), *A. glandulosa* Eastw. ( $4n$ , S) (900 m) and *A. manzanita* C. Parry ( $4n$ , NS) (700 m), from Hopland Research Station, Mendocino County; *A. pungens* Kunth var. *montana* (Eastw.) Munz ( $4n$ , NS) (350 m), *A. glandulosa* ( $4n$ , S) (400 m) from Carson Ridge, Marin County; *A. canescens* Eastw. ( $2n$ , NS) and *A. glandulosa* ( $4n$ , S) from Mt. Tamalpais, Marin County (600 m); *A. andersonii* A. Gray var. *imbricata* (Eastw.) J. Adams ex McMinn ( $2n$ , NS) and *A. tomentosa* (Pursh) Lindl. ( $4n$ , S) from San Pedro Valley Park, Pacifica, San Mateo County (60 m); *A. glauca* Lindl. ( $2n$ , NS) from Henry Coe State Park, Santa Clara County (750 m); *A. morroensis* Wiesl. Schreib. ( $2n$ , NS) from Montaña de Oro State Park, San Luis Obispo County (60 m); *A. rudis* Jeps. & Wiesl. ( $2n$ , S) from Burton Mesa, Santa Barbara County (85 m); and *A. pugens* Kunth ( $2n$ , NS) from Hwy. 79, San Diego County (1100 m). Nomenclature follows Munz (1959).

The 1986 percentage seed set values of all diploid and tetraploid species (regardless of habit) were combined and compared using Wilcoxon's rank-sum test (SAS 1987). Likewise, 1986 percentage seed set values for all sprouting and nonsprouting species (regardless of ploidy) were combined and compared using the same test. The 1987 data were not tested for significance because they do not differ substantially from 1986 data and because there are too few data to warrant statistical analysis.

TABLE 1. MEAN NUMBER OF OVULES PER OVARY, SEEDS PER FRUIT AND PERCENTAGE SEED SET FOR 1986 AND 1987 FOR SPROUTING AND NONSPROUTING  $2n$  AND  $4n$  *ARCTOSTAPHYLOS* SPECIES. Sample sizes are 100 ovaries and 50 fruit for 1986, and 50 ovaries and fruit for 1987 except where noted in parentheses.

Species	1986			1987		
	Ovules (N)	Seeds (N)	% Seed set	Ovules (N)	Seeds (N)	% Seed set
<b><math>2n</math>, NS</b>						
<i>A. stanfordiana</i>	6.10	4.20	68.8			
<i>A. canescens</i>	8.07	5.76	71.4			
<i>A. andersonii</i> var. <i>imbricata</i>	7.27	4.52	62.2	7.46	5.53 (15)	74.1
<i>A. glauca</i>	6.20	3.70	59.7	6.16	3.65 (17)	59.3
<i>A. morroensis</i>	7.29	5.32	73.0			
<i>A. pungens</i>			$\bar{X}$ = 69%	6.12	4.90	80.1 $\bar{X}$ = 71%
<b><math>2n</math>, S</b>						
<i>A. patula</i>	6.84	4.25 (12)	62.1			
<i>A. rudis</i>	5.86	4.62	78.8	6.12	4.24	69.3 $\bar{X}$ = 69%
<b><math>4n</math>, NS</b>						
<i>A. manzanita</i>	6.52	3.30	50.6			
<i>A. pungens</i> var. <i>montana</i>	7.06	4.90	69.4	6.58	4.17 (12)	63.4
			$\bar{X}$ = 60%	7.02	4.20 (10)	59.8 $\bar{X}$ = 62%
<b><math>4n</math>, S</b>						
<i>A. mewukka</i>	7.60	3.94 (17)	51.8			
<i>A. glandulosa</i> (Hopland)	7.40 (50)	3.70	50.0			
<i>A. glandulosa</i> (Carson Ridge)	7.56 (50)	3.84	50.8			
<i>A. glandulosa</i> (Mt. Tamalpais)	7.58	4.70	62.0			
<i>A. tomentosa</i>	7.89	4.50 (15)	57.0	7.70 (10)	2.50 (10)	32.5 $\bar{X}$ = 32%
			$\bar{X}$ = 54%			
			$\bar{X}$ = 68%* (SD = 7.0, N = 7)			
			$\bar{X}$ = 56%* (SD = 7.4, N = 7)			
			NS			
			S			

\* Differences between  $2n$  and  $4n$  species significant at  $P < 0.01$ .  
Differences between NS and S species not significant.

## RESULTS

Mean number of ovules per ovary, seeds per fruit and percentage seed set values for 1986 and 1987 are summarized in Table 1. The values for mean number of ovules per ovary in 1987 were all within 96% of 1986 values, but the mean number of seeds per fruit varied between years from 56% to 99%. The variation between years may be due to environmental variability during seed set within a site between years.

Overall, in each year the average percentage seed set values were higher for  $2n$  species than for  $4n$  species ( $P < 0.01$  for 1986) and  $4n$  sprouters had the lowest average seed set. Differences between sprouting and nonsprouting species in percentage seed set in 1986 were not significantly different. The four types of species for 1986 ranged from high to low in this order:  $2n, S > 2n, NS > 4n, NS > 4n, S$ ; and for 1987 in this order:  $2n, NS > 2n, S > 4n, NS > 4n, S$ . Within sites, the lowest percentage seed set values consistently belonged to  $4n$  sprouters. For example, at Hopland, where a  $4n$  nonsprouter occurred with a  $2n$  nonsprouter and a  $4n$  sprouter, percentage seed set ranged accordingly:  $2n, NS > 4n, NS > 4n, S$ .

## DISCUSSION

Comparisons among several sets of sprouting and nonsprouting tetraploid ( $4n$ ) and diploid ( $2n$ ) *Arctostaphylos* species revealed that tetraploids showed significantly reduced percentage seed set, and that seed set was lowest among sprouting  $4n$  species (Table 1). Sterility and polyploidy were discussed by Stebbins (1947, 1950, 1980) and evidenced in the work of Birari (1980). Polyploid species often show reduced fertility (deWet 1980), usually due to meiotic chromosomal irregularities and cytologically unbalanced gametes (Stebbins 1971). The absence of sterility in old, established polyploids is probably due to selection in the past for genetic changes that led to progressive "diploidization" so that meiotic pairing resembles that of diploids (Stebbins 1947, 1950). Alternatively, reduced seed fertility may be overcome by asexual reproduction, which may be the case for  $4n$  sprouting *Arctostaphylos* species. Reduced fertility also has been found in some polyploid species where regular meiosis was observed; the lower fertility was attributed to physiological disturbances (Tal 1980).

In this study, we found consistently higher percentage seed set in  $4n$  nonsprouting species than in  $4n$  sprouters. These results seem contrary to what we expected, which was equal seed set between  $4n$  sprouters and nonsprouters. However, nonsprouters suffer the risk of becoming eliminated upon disturbance unless they reproduce by seed. It may be, then, that selection for "diploidization" is stronger

in  $4n$  nonsprouting species than in sprouting species. Sprouting species are usually well-established in their habitats because they have retained or developed the ability to continuously resprout after fires. Therefore, selection for increased ability to set seed among  $4n$  sprouting species may not be as strong as for  $4n$  nonsprouting species.

The high incidence of reduced seed set among  $4n$  species and especially in  $4n$  sprouting species suggests that the number of seeds produced and seen in the seed banks of *Arctostaphylos* species is largely associated with the genetics of these organisms rather than their ecological mode of regeneration. It would be erroneous to interpret these patterns simply in terms of life history selection. The evolution of ecological differences between sprouting  $4n$  and non-sprouting  $2n$  species is probably largely a result of their ploidal history as well as ecological conditions.

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## NOTES

NOMENCLATRURAL CHANGE IN *SISYRINCHIUM DOUGLASII*. —Anita F. Cholewa, Department of Plant Biology, University of Minnesota, St. Paul, MN 55108 and Douglass M. Henderson, Department of Biological Sciences, University of Idaho, Moscow, ID 83843.

Recent phylogenetic work in *Sisyrinchium* and its relatives by Goldblatt et al. (1990, *Systematic Botany* 15:497–510) has revived the genus *Olsynium*. The latter name was first used by Rafinesque (1836, *New flora and botany of North America* 1:72) and generally included those species with terete stems, non-equitant leaves, pink to purple flowers, and a filament tube somewhat inflated at the base. The only North American species is *Olsynium douglasii* (A. Dietr.) Bickn., found in the Pacific Northwest, the northern Intermountain Region, and California. The resurrection of the genus, with which we fully agree, requires that the following new combination be made.

- OLSYNIUM DOUGLASII** (A. Dietr.) Bickn. var. **INFLATUM** (Suksd.) Cholewa & Henderson, comb. nov. —TYPE: USA, Washington, Spangle, 24 April 1916, *Suksdorf 8507* (lectotype designated in Cholewa & Henderson [1985, *Brittonia* 37:163–164]; WS!) —*Olsynium inflatum* Suksd., *Werdenda* 1:8. 1923. —*Sisyrinchium inflatum* (Suksd.) St. John, Report of the Provincial Museum of Natural History B.C. 1930:12. 1931. —*Sisyrinchium douglasii* A. Dietr. var. *inflatum* (Suksd.) P. Holmgren, *Intermountain Flora*, Vol. 6:540. 1977.
- SISYRINCHIUM INFLATUM** (Suksd.) St. John f. **ALBA** St. John, Rep. Prov. Mus. Nat. Hist. B.C. 1930:12. 1931. —TYPE: USA, Washington, Yakima Co., Glade Creek, 3 km N of Bluelight. 12 Apr 1929, *St. John et al. 9785* (holotype: WS!).
- SISYRINCHIUM INALATUM** A. Nelson, Bot. Gaz. 54:136. 1912. —TYPE: USA, Idaho, Owyhee Co., Silver City, 17 Jun 1911, *Macbride 909* (holotype: RM).

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